

The coevolution of warning signals

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It has long been recognized that defended prey tend to be conspicuous. Current theories suggest that the association ('aposematism') has arisen because predators more readily learn to avoid attacking defended phenotypes when they are conspicuous. In this paper, I consider why such psychology has evolved. In particular, I argue that aposematism may have evolved not because of an independent and pre-existing receiver bias, but because the conspicuousness of a prey item provides a reliable indicator of its likelihood of being defended. To develop my case I consider how warning signals might coevolve in a system containing a number of predators, whose foraging behaviour is also subject to selection. In these cases, models readily show that the greater the conspicuousness of a novel prey item, the more likely that it has been encountered by other predators and survived. As a consequence, naive predators should be less likely to attack highly conspicuous novel prey on encounter, or at least more inclined to attack them cautiously. This adaptive predator behaviour will greatly facilitate the spread of aposematic phenotypes from extreme rarity, which in turn will enhance selection for forms of predator behaviour under which aposematism will coevolve even more readily.

Keywords: aposematism; warning coloration; neophobia; dietary conservatism

1. INTRODUCTION

It has long been recognized that defended prey tend to be conspicuous in some way, typically by sight, sound or behaviour (Wallace 1867; Darwin 1874; Poulton 1890). One explanation for this phenomenon, termed aposematism (Poulton 1890), is that conspicuousness capitalizes on the inherent receiver biases of predators. Thus, predators more readily learn to associate prey defensiveness with conspicuousness, and they forget this association less easily (Guilford 1988, 1990; Endler 1991; Speed 2000). These receiver-orientated theories have found broad support (see Gittleman & Harvey 1980; Gamberale & Tullberg 1996), but they do not in themselves explain *why* predators exhibit these particular psychological characteristics.

While the majority of earlier studies have considered the outcome of selection on prey conspicuousness by a single predator foraging according to a fixed set of behavioural rules, I consider elements of a system in which both prey conspicuousness and predator behaviour are subject to selection. Predators may indeed find that experiences associated with conspicuousness signals are more memorable, but it is important to note that the conspicuousness of a prey item also affects its ease of detection. In particular, any overtly conspicuous prey item that is encountered by a predator has probably already been seen by other predators and somehow survived. Similarly, consider a predator that arrives in a new area containing several experienced predators. If there are any common conspicuous prey species in the area, then such prey types are probably defended in some way because otherwise they could not have readily achieved high densities. In both instances it is conceivable that there would be mutually beneficial selection on predators to evolve a predisposition to reacting with greater caution towards conspicuous signals, since they indicate an increased likelihood that a given phenotype is defended. I have attempted

to quantitatively evaluate the validity of these encounter-based arguments, and identify specific mechanisms under which such a coevolutionary process leads to the evolution of aposematism.

The coevolutionary models I present differ in three important ways from the majority of earlier theoretical studies (Harvey *et al.* 1982; Sillén-Tullberg & Bryant 1983; Leimar *et al.* 1986; Yachi & Higashi 1998; Servedio 2000; Speed 2001). First, I consider the evolution of warning signals in a model system containing more than one individual predator. I have made this assumption not only because I believe it is more realistic, but also because the signalling mechanism I describe will have no meaning if there is only a single predator in the model universe. Second, I consider systems that contain many prey species, some of which are defended and some not, rather than a single species of defended prey (see also Leimar *et al.* 1986; Servedio 2000). I suggest that when prey species are diverse and heterogeneously distributed, then many novel prey types that are encountered by predators will not be mutants of familiar sympatric prey, but rare immigrants of new species.

Finally, I focus on understanding the evolutionary basis of the initial responses of predators towards novel prey items, although I note that a predator's ability to subsequently learn about particular prey types may be related, to some extent, to its initial reaction towards those prey (Schuler & Roper 1992). Of course, one would expect that the ability of predators to remember and react to their experiences with particular prey types would also be directly subject to selection, but for simplicity I do not consider this phenomenon here. Despite this omission, the initial response of predators towards novel prey may, in itself, play an important role in determining whether aposematic phenotypes spread from extreme rarity ('stage 1' of Speed 2001). Marples *et al.* (1998) made such a case when they found that novel conspicuous pastry baits did

not always experience higher predation rate by birds than more familiar cryptic forms. Lindström *et al.* (2001) came to similar a conclusion when they found that great tits (*Parus major*) that had experience of palatable cryptic prey were reluctant to attack novel conspicuous prey.

2. ANALYTICAL MODEL

Consider an area containing n predators (of the same species or different species). Individuals of novel prey species occasionally immigrate into this area, and q is the probability that any given immigrant is undefended. Defended prey items may carry unpalatable toxins, or a sting for instance, or they may simply be very difficult to catch. The novel immigrants vary in conspicuousness, a trait measured by their probability, p , of detection by any predator that comes within a fixed vicinity (in turn determined by the prey's visible appearance and behaviour). Predators encounter prey at random, and it is assumed that any new immigrant will successfully establish (e.g. lay its eggs) in the area if it can survive individual predators searching within its vicinity on t separate occasions. In this first model, x_p predators attack novel prey of conspicuousness p while y_p predators do not attack these prey ($x_p + y_p = n$). Defended and undefended prey survive attacks from predators with probabilities s_d and s_u , respectively. I let the mean benefit to a predator that successfully captures an undefended prey item be b , and the mean cost of attacking a defended prey item be c . To begin with, I make the simplifying assumption that any predator which attacks a prey item that somehow escapes does not gain any information about the prey's suitability should it encounter that prey again: this assumption is later modified.

If the above conditions hold then it is easy to show that the probability (ψ) that any novel immigrant of conspicuousness p encountered by a predator is undefended is given by $\theta / (\theta + \phi)$, where

$$\theta = \sum q \{ (1 - p) + p(x_p/n)s_u + p(y_p/n) \}^j$$

and

$$\phi = \sum (1 - q) \{ (1 - p) + p(x_p/n)s_d + p(y_p/n) \}^j$$

for $j = 0, 1, \dots, t - 1$. Here θ and ϕ are proportional to the total number of surviving undefended and defended prey of conspicuousness p that are likely to be encountered by predators over t separate search events. The value of ψ is only equal to q if $s_u = s_d$, $p \rightarrow 0$, $q \rightarrow 1$, $x_p = 0$ or $t = 1$ (no other individual encounters the prey item before it establishes). In general, if $x_p > 0$ and $s_u < s_d$, then the more conspicuous a newly encountered novel prey item is, the more likely it is that it will be defended (figure 1). This arises simply because when prey are frequently encountered (i.e. conspicuous) then they will be more likely to survive if they are defended.

Given the above conditions, it is possible to determine the evolutionarily stable combination of predatory strategies that should evolve for dealing with novel immigrants. While the payoff to any predator that does attack novel immigrants of conspicuousness p will always be 0 with respect to this prey type, the payoffs to predators that attack these novel prey will depend, in part, on how many other predators adopt this strategy, specifically $b(1 - s_u)\psi$

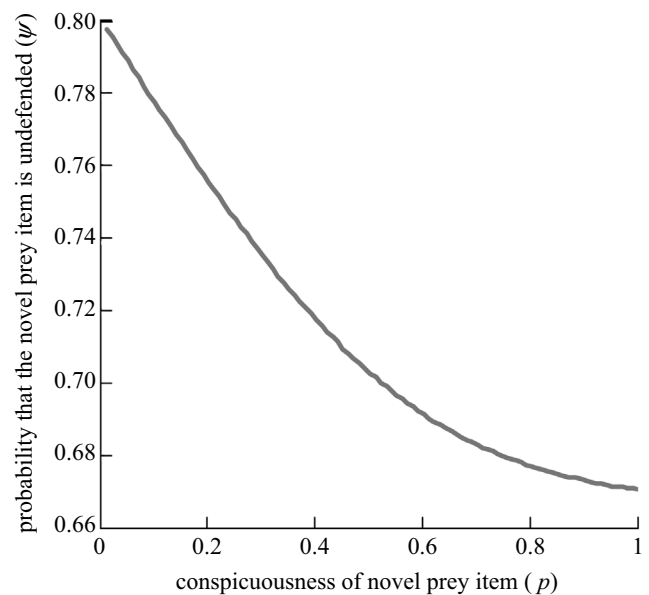


Figure 1. If defended prey survive better on attack than undefended prey and conspicuous prey are more likely to be encountered by predators, and novel cryptic prey are more likely to be undefended than novel conspicuous prey. Parameter values: $n = 30$, $q = 0.8$, $t = 8$, $s_u = 0.2$, $s_d = 0.6$, with all predators attacking novel prey ($x_p = 30$).

$- c(1 - \psi)$. Sometimes the costs and benefits will be such that evolutionarily stable strategy (ESS) solutions are the same whatever the conspicuousness of novel prey. For instance, if ψ is consistently greater than $c / \{b(1 - s_u) + c\}$ then all novel prey should be attacked whatever their conspicuousness. However as figure 1 shows, ψ is often highly dependent on p . Under a wide range of conditions, all predators will maximize their payoffs if they attack highly cryptic novel prey items (a pure evolutionarily stable strategy $\{x_p = n, y_p = 0\}$) (figure 2). In contrast, the ESS set when highly conspicuous novel prey are encountered is typically a mixture of attackers and non-attackers [$x_p = \alpha$, $y_p = n - \alpha$, $0 < \alpha < n$] (figure 2).

There are several different ways in which predators might achieve these ESS solutions. Of course, there may be an element of direct natural selection acting on the initial response. However, if conditions vary then there may be strong selection for a more versatile strategy in which predators develop an ability to generalize, learning over time to attack/reject novel prey types with particular conspicuousness because on average such prey are profitable/unprofitable (see Braveman 1978; Lindström *et al.* 2001). Whatever the precise mechanisms, it is clear that there are many instances where predators would gain a selective advantage if they could evolve a psychological sensitivity towards prey conspicuousness, which in turn would allow them to behave differently towards novel prey with different prominences.

The adaptive behaviour of predators towards novel prey will almost certainly have important implications for the evolution of aposematism. It is easy to show that in all ESS solutions in which there is a mixture of attackers and non-attackers then defended prey items will have an identical survival rate whatever their conspicuousness to predators. For instance, if we kept the parameters the same as in figure 2 but raised the cost, c , of attacking defended

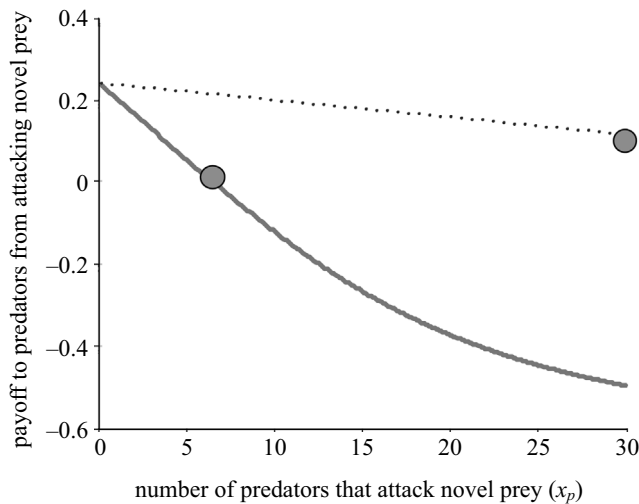


Figure 2. Payoffs to predators from attacking novel prey on encounter, as a function of the number of predators that attack these prey types. Parameter values: $n = 30$, $q = 0.8$, $t = 10$, $s_u = 0.2$, $s_d = 0.8$, $b = 1$, $c = 2$. Circles indicate the x_p element of the evolutionarily stable combination of predatory strategies, and the resultant mean payoffs to all predators. When novel prey are cryptic (dotted line) (here $p = 0.1$) then they should be attacked by all predators, but when novel prey are conspicuous (solid line) (here $p = 0.9$) then an ESS arises when only a few predators (in this case approximately six) attack these prey types on encounter. As a result of this optimal predator behaviour, novel defended prey will have a probability of 0.817 (if cryptic) or 0.672 (if conspicuous) of establishing a population. Similarly, novel undefended prey will have a probability of 0.434 (if cryptic) or 0.183 (if conspicuous) of establishing a population.

items to 3, then all defended novel prey items in the conspicuousness range $0.03 \leq p \leq 1$ would have the same probability of establishing. Since cryptic novel prey will never have a lower chance of survival to establishment than conspicuous novel prey, then this particular model cannot by itself explain why conspicuousness might be actively selected for in defended prey, but it does help explain why it is not always selected against.

3. MODEL REFINEMENTS

Several aspects of the above model are overly simplistic, or at least refer to a particular set of circumstances. I now consider some important changes to the model structure, and the implications of these refinements for the evolution of aposematism. Although the coverage of these modifications is necessarily brief, I hope that this discussion demonstrates the value of adopting a coevolutionary approach and the need to consider systems containing several prey species and more than one individual predator.

(a) Runaway coevolution

One very important limitation of the basic model is that it assumes that the initial probability q of a novel immigrant being undefended is independent of p . However, immigrants must come from somewhere. Eventually all novel prey types that survive to establishment are likely to reach densities at which it will pay all predators to sample them. Once predators discover that a particular conspicuous prey type is undefended then this population is

unlikely to persist, or at least achieve a significant size and generate many dispersers. One direct consequence of this is that once aposematic species begin to establish and disperse (and conspicuous undefended species do not), then their presence would help generate selection in predators for an even greater sensitivity and phobia towards conspicuousness, under which further aposematic phenotypes could evolve. The importance of this process was recognized by Turner (1984) who argued, 'once bright coloration becomes the badge of toxic prey, there will be selection on predators to have an innate tendency to avoid such colours or to learn rapid avoidance of them' (p. 143).

To demonstrate the power of this coevolutionary runaway process, consider a case in which $n = 20$, $t = 5$, $b = 1$, $c = 2$, $s_u = 0.3$, $s_d = 0.6$. If $q = 0.8$ for $p = 0.1$ but $q = 0.7$ for $p = 0.9$ then all predators should attack the cryptic novel prey on encounter, but no predator should attack the conspicuous novel prey on encounter. Such behaviour will clearly favour the establishment of aposematic forms (as well as undefended cheats, at least initially), and will act to increase further the reluctance of other predators that receive these aposematic prey as immigrants, to attack novel conspicuous prey. Of course, we still have to explain how aposematism initially evolved somewhere, hence the basic model with an analogous sympatric process. However, the coevolutionary runaway effect is so powerful that it will tend to facilitate the evolution of aposematism through continued selection on predator perceptions and behaviour, even if aposematism initially arises by chance in certain areas and there is typically no more than a single predator per foraging area.

(b) Benefits of overt conspicuousness

Even if actively advertising one's lack of interest in being discovered by predators brings no net increase in predator-mediated survivorship to a defended novel immigrant, then it may well yield other benefits, which, together with adaptive dietary conservatism, may help tip the balance in favour of aposematism. For instance, defended prey that actively advertise their frequency of encounter with predators will not have to invest their time and energy in vigilance, and may be able to forage in exposed areas that are simply not suitable for prey maintaining a degree of crypsis. Such an effect is easily incorporated into the basic model as an additional survivorship term (sa_p) that is independent of predator-mediated survivorship. In the specific case of the example in figure 2, then as long as $sa_{0.1}/sa_{0.9} < 0.848$ then a conspicuous defended novel prey would have a greater chance of surviving than a more cryptic form (the same would be less likely to apply for an undefended prey since it would require $sa_{0.1}/sa_{0.9} < 0.422$).

(c) Benefits of aggregation

It is easy to show that if prey items are aggregated, then aposematism is even more likely to evolve. To demonstrate this, consider the extreme case in which individual prey items are always killed on attack ($s_u = s_d = 0$). Any predator that encounters and consumes an item of aggregated undefended prey will most probably consume them all ($s_u = 0$ for aggregation as a whole), but any predator that attacked a defended prey item within a group would probably leave the rest ($s_d \approx 1$ for a large enough group

size). Given the very large difference between s_u and s_d as a group, and the even higher conspicuousness of an aggregation, then even fewer predators should attempt to attack novel conspicuous prey when they are aggregated, which may in turn facilitate their spread.

(d) Additional predatory strategies

If predators can adopt other behavioural strategies besides attacking or not attacking novel prey, then there are indeed particular circumstances in which defended prey would have greater chances of establishing a population in a new area if they were conspicuous. To demonstrate this, consider a population of n predators, this time with three predatory strategies. As before, x_p predators attack novel prey items of conspicuousness p , and y_p do not attack these prey types. However z_p predators attack these prey types cautiously ($x_p + y_p + z_p = n$). By attacking prey items cautiously, I assume that the mean cost of attempting to handle these prey if they are defended is reduced to $h c$ ($0 < h < 1$), yet defended and undefended prey are even more likely to escape capture (probabilities sc_d and sc_u respectively). While ψ and other parameters can easily be derived analytically, here the evolutionary dynamics are most easily demonstrated by simulation. In this case I have adopted the more realistic assumption that any predator that re-encounters a novel prey item that had survived its earlier attack(s) subsequently avoids attacking this prey item (if it was defended), or attacks this prey without caution (if the prey item was undefended).

As earlier, under a variety of conditions all predators evolved a tendency to attack cryptic novel immigrants without caution, since these prey types were unlikely to have been seen and attacked by others (figure 3a). In contrast, under the same conditions a stable combination of predatory strategies tended to evolve to deal with novel conspicuous prey: some individuals attacked these prey with caution, while others did not attack these prey types at all (figure 3b). Clearly, if any prey species could achieve near invisibility then it would always have a higher predator-mediated survivorship than a more conspicuous novel prey. Yet these simulations (and supporting analytical work) indicate that novel defended prey will sometimes have a lower chance of surviving if they are reasonably cryptic (in this case $p = 0.05$) than if they were much more conspicuous (figure 4). In contrast, in these particular simulations, undefended novel prey typically had a much greater chance of surviving to establishment if they were cryptic (figure 4).

(e) Other ways in which sympatric predators filter out conspicuous undefended prey

Finally, it is important to note that there may be several alternative ways in which intense conspicuousness-dependent sorting of undefended and defended prey types might arise in systems containing more than one sympatric predator, even if technically $s_u = s_d$ from a single attack. For instance, any prey item that escapes a predator's initial attack may continue to be pursued by the same predator, particularly if the predator has not experienced a defensive reaction by the prey on its initial encounter. This secondary filtering of defended from undefended prey is probably more intense for conspicuous than cryptic prey, since cryptic prey will be more likely to evade immediate recap-

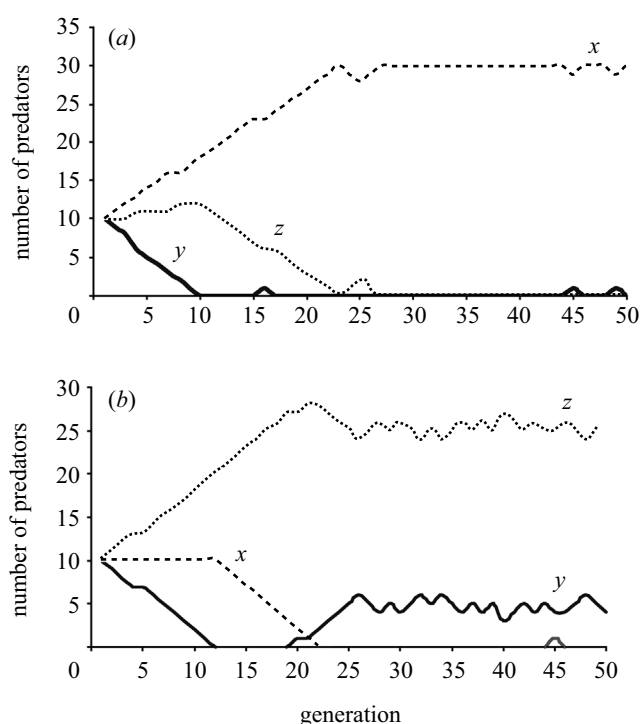


Figure 3. Evolution of predatory strategies under simple dynamical rules. Each generation, 10 000 novel immigrants of a particular conspicuousness class were introduced in turn. At the end of each generation the number of predators with the strategy that performed best was increased by 1, while the number of predators with the strategy that performed worst was decreased by 1. Mutations (in which a randomly selected predator was given a randomly selected strategy) occurred with probability 0.2 per generation. Parameter values: $n = 30$, $q = 0.8$, $t = 10$, $s_u = 0.1$, $s_d = 0.2$, $sc_u = 0.4$, $sc_d = 0.9$, $h = 0.4$, $b = 1$, $c = 2$. Initial conditions: $x_p = y_p = z_p = 10$. (a) When novel prey were cryptic ($p = 0.1$) then all predators evolved a tendency to attack these prey directly on encounter. (b) When novel prey were conspicuous ($p = 0.9$) then some predators evolved to attack these prey types cautiously, while other predators did not attack these prey at all. Solid line, y : do not attack novel prey; dotted line, z : attack novel prey cautiously; dashed line, x : attack novel prey directly.

ture. In this case: (i) defended prey will survive repeated encounter sequences much better than an undefended prey, and (ii) the survivorship of undefended prey will decline with their increasing conspicuousness, both of which will strongly favour the evolution of conspicuousness-dependent predatory behaviour and the subsequent evolution of aposematism.

4. DISCUSSION

The models presented here indicate that aposematism can readily coevolve if predator behaviour is also subject to selection. Specifically, if a cryptic defended prey species was mobile, such that prey individuals regularly move into areas where they are likely to regularly encounter naive predators, then there are a range of plausible conditions under which a highly conspicuous mutant would spread far faster than a more cryptic conspecific. Like the majority of earlier studies, I believe that predator psychology will play an important role in facilitating this pro-

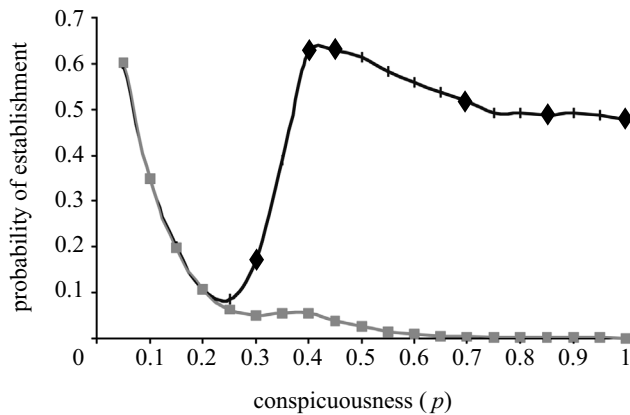


Figure 4. The mean probability of a novel prey type surviving potential encounters calculated in the last generation of 50 separate 50-generation simulations in which predators evolved strategies according to the conditions described in figure 3. As predators tended to attack novel conspicuous prey cautiously, and defended prey have a high chance of surviving cautious attacks, then novel defended prey have a higher probability of surviving to establishment if they are conspicuous. Filled diamonds, novel defended prey; filled squares, novel undefended prey.

cess, but I question whether defended prey have tended to evolve conspicuousness simply because that happens to have been the type of signal that predators *a priori* find easiest to learn. Aposematism occurs in many species, with conspicuousness manifesting itself in a variety of sensory modalities to a taxonomically diverse array of predators. It is possible that all these predators have the same independent pre-existing receiver biases towards conspicuous signals, but it is perhaps more likely that these receiver biases have arisen for a common selective purpose. Conspicuous prey items are more likely to be defended at the outset, since in the absence of a receiver bias, such prey are more likely to have already survived despite frequent encounters with predators. As I have argued, once predators begin to adapt to the association, then aposematism can even more readily develop in a self-enforcing coevolutionary process in which signal reliability is maintained more by dynamics (populations of conspicuous undefended prey are unlikely to generate many dispersers) than by the survivorship of any particular novel immigrant.

As the first model shows, one way in which this form of encounter-based signalling may be initiated arises when there is more than one sympatric predator, and when defended prey are, on average, more likely to survive attacks than undefended prey ($s_u < s_d$, either as individuals, or an aggregated group). It is now well known that defended prey species regularly survive attack by predators (Boyden 1976; Järvi *et al.* 1981; Wiklund & Järvi 1982; Guilford & Dawkins 1993), in part because defences such as toxins are often located in the outer parts of their bodies (Brower & Glazier 1975). Almost by definition, undefended prey should be less likely to survive attacks by predators, so the condition $s_u < s_d$ appears entirely reasonable. I am not aware of any study that provides a direct test of this relationship, but Boyden (1976), for instance, found that *ca.* 20% of distasteful *Heliconis* butterflies survived attacks by naive lizards, while no palatable *Anartia* butterflies survived similar attacks.

In broad anthropocentric terms, the models proposed suggest that predators should be wary of overtly conspicuous prey because they are 'too good to be true'. As such, the theory may explain, at a fundamental level, why naive predators tend to show an initial reluctance to attack conspicuous prey (see Schuler & Hesse 1985; Sillén-Tullberg 1985; Schuler & Roper 1992; Roper & Cook 1989; Marples *et al.* 1998; Rowe & Guilford 1999; Lindström *et al.* 1999a) and why predators appear less inclined to attack aggregated aposematic prey compared with solitary aposematic prey (Gagliardo & Guilford 1993; Gamberale & Tullberg 1998). As the responses of predators to conspicuous prey often constitute a mixed ESS solution, then the model may also account for the surprisingly high genetic variation in dietary conservatism towards novel aposematic prey (Marples & Brakefield 1995; Marples *et al.* 1998).

My final model considers the outcome of frequency-dependent selection in which there were three particular predatory strategies: do not attack novel prey of a particular conspicuousness, attack them cautiously and attack them directly. In support, Sillén-Tullberg (1985) found that the red forms of a distasteful *Lygaeus* bug survived a far greater proportion of attacks by naive great tits (*Parus major*) than more cryptic forms, and suggested that the conspicuously coloured larvae 'survived better because they were handled more cautiously by the birds' (p. 413). Indeed, this same study found that the conspicuous morph had a better overall chance of surviving than its cryptic conspecifics. Similarly, Schuler & Hesse (1985) found that while young chicks directed their first pecks at warningly-coloured (black and yellow) and olive-coloured mealworms with the same probability, they consumed warningly-coloured ones at a much lower rate due to a greater inhibition in their form of attack. As we have seen, if the effect of the conspicuousness is to generate a 'go slow' (Guilford 1994) reaction, rather than 'stop', in a proportion of predators, then proportionately fewer undefended prey items will survive if they are conspicuous. Conversely, since the 'handle with care' strategy is only selected for highly conspicuous novel prey then it may help to explain why defended prey sometimes appear so overtly conspicuous.

My theory differs from earlier theories because it suggests that aposematism should arise relatively rapidly, rather than gradually, which is consistent with the recent experimental findings of Lindström *et al.* (1999b). My approach emphasizes the responses of predators to novel prey types (which may well be shaped to a degree by an ability of predators to generalize from previous experience). However, I recognize that learning by direct experience probably plays an extremely important role in facilitating the evolution of aposematism in the subsequent increase phase of an aposematic phenotype ('stage 2' of Speed 2001). At this stage for instance, even a conspicuous defended prey that could not survive any attack but which had slow-acting toxins may also be allowed to spread. Nevertheless it is important to note that even here neophobia, and the subsequent direct learning process, may be closely interrelated, in that a stimulus that predators are reluctant to attack may also favour faster avoidance learning if the prey item proves to be unprofitable (Schuler & Roper 1992).

In an earlier paper Guilford & Dawkins (1993) argued

that warning coloration was unlikely to be a handicap (Zahavi 1991; Zahavi & Zahavi 1997), in the strict sense of a form of 'signal extravagance', that only individuals of defended species could afford to invest in (see also Grafen 1990). Whether warning signals are considered as biological handicaps or not may depend on one's interpretation of the term. For instance, some have argued that handicaps should be regarded as completely honest reflections of an individual's ability to bear costs, and therefore cannot be mimicked (e.g. Archetti 2000). In the models presented there is clearly no inherent biological connection between the conspicuousness of a prey type and its defendability. However, I argue that, following the actions of predators, prey conspicuousness is indeed given some meaning as a signal of probable defensibility. In general, selection to exhibit reliable indicators of defensibility may explain why it might pay defended individuals to flaunt their lack of vulnerability through blatant conspicuousness, just as some birds may sing (Cresswell 1994), or some gazelles strut (Zahavi & Zahavi 1997), when approached by a predator.

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